MarLIN

Marine Information Network

Information on the species and habitats around the coasts and sea of the British Isles

Mastocarpus stellatus and *Chondrus crispus* on very exposed to moderately exposed lower eulittoral rock

MarLIN – Marine Life Information Network
Marine Evidence–based Sensitivity Assessment (MarESA) Review

Dr Heidi Tillin

2016-03-30

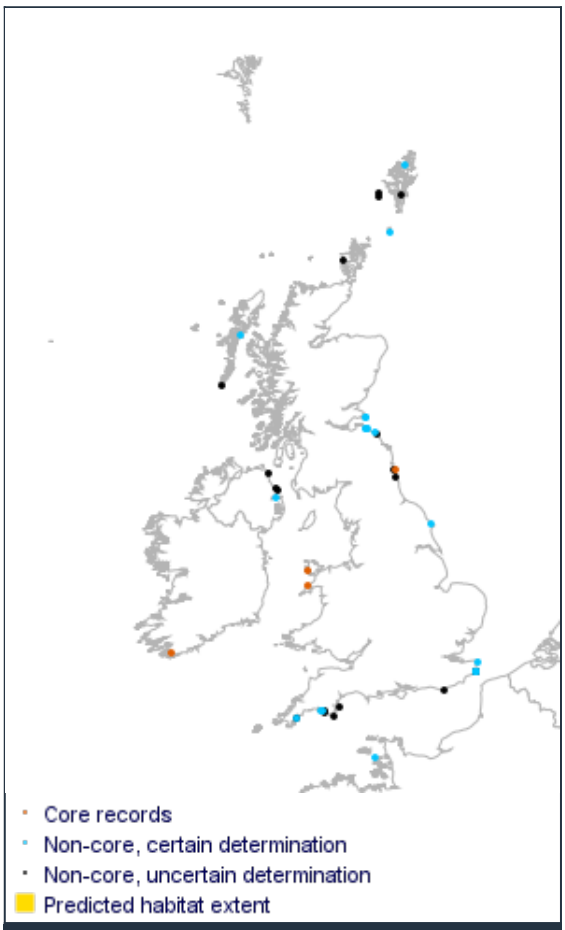
A report from:
The Marine Life Information Network, Marine Biological Association of the United Kingdom.

Please note. This MarESA report is a dated version of the online review. Please refer to the website for the most up-to-date version [https://www.marlin.ac.uk/habitats/detail/11]. All terms and the MarESA methodology are outlined on the website (https://www.marlin.ac.uk)

This review can be cited as:
Tillin, H.M. 2016. [Mastocarpus stellatus] and [Chondrus crispus] on very exposed to moderately exposed lower eulittoral rock. In Tyler-Walters H. and Hiscock K. (eds) *Marine Life Information Network: Biology and Sensitivity Key Information Reviews*, [on-line]. Plymouth: Marine Biological Association of the United Kingdom. DOI https://dx.doi.org/10.17031/marlinhab.11.1

(page left blank)

***Mastocarpus stellatus* and *Chondrus crispus* on very exposed to moderately exposed lower eulittoral rock**
Photographer: David Connor



17-09-2018
Biotope distribution data provided by EMODnet Seabed Habitats (www.emodnet-seabedhabitats.eu)

Researched by Dr Heidi Tillin **Refereed by** Admin

Summary

UK and Ireland classification

EUNIS 2008	A1.125	*Mastocarpus stellatus* and *Chondrus crispus* on very exposed to moderately exposed lower eulittoral rock
JNCC 2015	LR.HLR.FR.Mas	*Mastocarpus stellatus* and *Chondrus crispus* on very exposed to moderately exposed lower eulittoral rock
JNCC 2004	LR.HLR.FR.Mas	*Mastocarpus stellatus* and *Chondrus crispus* on very exposed to moderately exposed lower eulittoral rock
1997 Biotope	LR.MLR.R.Mas	*Mastocarpus stellatus* and *Chondrus crispus* on very to moderately exposed lower eulittoral rock

Description

Exposed to moderately exposed lower eulittoral vertical to almost horizontal bedrock characterized by a dense turf of *Mastocarpus stellatus* and *Chondrus crispus* (either together or

separately). Beneath these foliose seaweeds, the rock surface is covered by encrusting coralline algae and the barnacle *Semibalanus balanoides*, the limpet *Patella vulgata* and spirorbid polychaetes. Other seaweeds including the red *Lomentaria articulata* and *Osmundea pinnatifida*, *Palmaria palmata*, *Corallina officinalis* and coralline crusts. The wrack *Fucus serratus* and the green seaweeds *Ulva intestinalis* and *Ulva lactuca* may also be present though usually at a low abundance. Although both *Mastocarpus stellatus* and *Chondrus crispus* are widespread in the lower eulittoral and the sublittoral fringe, they occur only infrequently in a distinct band, or in large enough patches, to justify separation from Fser.R. Consequently, where only small patches of these species occur within a larger area of mixed red algal turf, then records should be assigned to more general mixed red algal turf biotope (Coff; Him). *Mastocarpus stellatus* can be present in high abundance in a number of biotopes (Coff: Him; Fser.R etc.) found on the shore. At least one other species normally co-dominates and records should be assigned to the appropriate biotope. Caution should be taken regarding the characterizing species list due to the low number of records. More information needed to validate this description (JNCC, 2015).

Depth range

Lower shore

Additional information

-

Listed By

- none -

Further information sources

Search on:

G G JNCC

Sensitivity review

Sensitivity characteristics of the habitat and relevant characteristic species

The biotope description and characterizing species are taken from Connor *et al*., (2004). The biotope is characterized by a dense turf of *Mastocarpus stellatus* and *Chondrus crispus* (either together or separately). As the presence of *Mastocarpus stellatus* and *Chondrus crispus* define the biotope the sensitivity assessments are focussed on these species. Beneath these foliose seaweeds the rock surface is covered by encrusting coralline algae and the barnacle *Semibalanus balanoides*, the limpet *Patella vulgata* and spirorbid polychaetes. Other seaweeds present include the red algae *Lomentaria articulata* and *Osmundea pinnatifida*, *Palmaria palmata*, *Corallina officinalis* and coralline crusts. The wrack *Fucus serratus* and the green seaweeds *Ulva intestinalis* and *Ulva lactuca* may also be present though usually at a low abundance. The species associated with the turf of *Mastocarpus stellatus* and *Chondrus crispus* occur in a number of biotopes and are not key characterizing species but do contribute overall to species richness, diversity and ecosystem function. The sensitivity of these species is considered generally in the sensitivity assessments: more information for these species can be found in other biotope assessments within this website.

Resilience and recovery rates of habitat

Recovery of the biotope requires the recovery of a recognizable biotope based on the biotope description from Connor *et al*. (2004) and is thus dependent on the recovery of a macroalgal turf dominated by *Mastocarpus stellatus* and other turf forming red seaweeds. The presence of the associated invertebrate species does not define recovery but these species may be important structuring factors through grazing control on algae species and their recovery is also discussed.

The turf forming red algae may recover through repair and regrowth of damaged fronds or via recolonization of rock surfaces where all the plant material is removed. The red algae have complex life histories and exhibit distinct morphological stages over the reproductive life history. Alternation occurs between asexual spore producing stages (tetrasporophytes) and male and female plants producing sexually. Life history stages can be morphologically different or very similar. The tetrasporophyte phase of *Mastocarpus stellatus* is known as the Petrocelis and is a flat crust, capable of growing laterally and covering extensive areas. The gametophtyes and tetrasporphytes of *Chondrus crispus* are relatively similar but the holdfasts of individual *Chondrus crispus* can coalesce over time and can form an extensive crust on rock (Taylor *et al*., 1981). Other red algae found within the biotope also have life stages that include prostrate creeping bases e.g. encrusting corallines, *Corallina officinalis* and *Osmundea pinnatifida* whereas in other species such as *Palmaria palmata*, the thallus or fronds arise from a small discoid holdfast. The basal crusts and crustose tetrasporphytes are perennial, tough, resistant stages that may prevent other species from occupying the rock surface and allow rapid regeneration. They may therefore provide a significant recovery mechanism. For some red algae, such as *Corallina officinalis*, the basal crust is more resistant to some pressures than the fronds and provides a mechanism for recovery following exposure to pressures that remove the fronds. Previous studies on *Chondrus crispus* indicate that the gametophytes (erect fronds) and tetrasporophytes (crusts) exhibit similar physiological responses to salinity and temperature (Mathieson & Norall 1975, Chopin & Floc'h 1992). However, the physiological tolerances of the crust and gametophytes of *Mastocarpus stellatus* varied widely (Dudgeon *et al*., 1995). Therefore for *Chondrus crispus* the bases may, in some instances, not survive to support recovery where the fronds are removed. Where holdfasts and basal crusts are removed, recovery will depend on recolonization via spores. Norton (1992) reviewed dispersal by macroalgae and concluded that dispersal potential is highly variable,

recruitment usually occurs on a much more local scale, typically within 10 m of the parent plant. Hence, it is expected that the algal turf would normally rely on recruitment from local individuals and that recovery of populations via spore settlement, where adults are removed, would be protracted.

Growth rates of *Chondrus crispus* vary widely according to environmental conditions. Pybus (1977) reported mean growth for *Chondrus crispus* from Galway Bay of 0.33 mm/day, with little seasonal variation in growth rate. A similar rate of 0.37 mm/day was reported for plants from Maine, USA (Prince & Kingsbury, 1973). Measurements of in-situ growth rate in Maine, North America by Dudgeon *et a*l., (1995) found that *Chondrus crispus* are faster growing than *Mastocarpus stellatus* (mean growth 2.65 g/dry weight/m2/day compared with mean 1.04 g/dry weight/m2/day respectively). No measureable growth of *Mastocarpus stellatus* crusts was observed after a year (Dudgeon et al., 1995). Growth patterns vary seasonally with the highest biomass usually in late Spring or Summer and lowest in Winter (Fernández, & Menéndez, 1991).

Dickinson (1963) reported that *Chondrus crispus* was fertile in the UK from autumn to spring, but that the exact timings varied according to local environment. Similarly, Pybus (1977) reported that although carposporic plants were present throughout the year in Galway Bay, Ireland, maximum reproduction occurred in the winter and estimated that settling of spores occurred between January and May. In northern Spain, *Chondrus crispus* had reproductive capacity all year round but was greatest for gametophytes between November and March and for tetrasporophytes in April (Fernandez & Menendez, 1991). In Nova Scotia, Canada, cystocarps and tetrasporangia have been recorded on *Chondrus crispus* all year round with a reproductive peak from August to October (Scrosati *et al.*, 1994). However, spores failed to germinate below 5°C and so winter temperatures in Nova Scotia are unsuitable for spore germination. It was suggested therefore that simple counts of spore production do not adequately model reproductive potential (Scrosati *et al.*, 1994). Scrosati *et al.* (1994) also commented that viability of spores was low (<30%) and suggested that reproduction by spores probably does not contribute much to maintenance of the intertidal population of *Chondrus crispus* in Nova Scotia, compared to vegetative growth of gametophytes.

Pybus (1977) estimated that *Chondrus crispus* from Galway Bay, Ireland, reached maturity approximately 2 years after the initiation of the basal disc, at which stage, the fronds were approximately 12 cm in length. The fronds of *Chondrus crispus* typically have a life of 2-3 years (Taylor, cited in Pringle & Mathieson, 1986) but may live up to 6 years in sheltered waters (Harvey & McLachlan, 1973).

Most of the evidence for recovery of *Chondrus crispus* is based on experiments that simulate the effects of different harvesting mechanisms and intensities (Macfarlane, 1952; Mathieson & Burns, 1975). Due to similarities in biology it is suggested that these recovery rates may also be applicable to *Mastocarpus stellatus*. Macfarlane (1952) in a series of experiments identified that where *Chondrus crispus* was removed by cutting of fronds or thorough raking (leaving the crusts undamaged) the turf had recovered and there were no notable differences bwetween the experimental areas and control sites. However, where the crusts were removed by scraping or damaged the experimental plots were still recovering nearly two years after the treatment. Following experimental harvesting by drag raking where (holdfasts and small blades were undamaged) in New Hampshire, USA, populations recovered to 1/3 of their original biomass after 6 months and totally recovered after 12 months (Mathieson & Burns, 1975). The authors suggested that control levels of biomass and reproductive capacity are probably reestablished after 18 months of regrowth (where crusts are not removed). It was noted however, that time to recovery was much extended if harvesting occurred in the winter, rather than the spring or

summer (Mathieson & Burns, 1975).

Minchinton *et al.* (1997) documented the recovery of *Chondrus crispus* after a rocky shore in Nova Scotia, Canada, was totally denuded by an ice scouring event. Initial recolonization was dominated by diatoms and ephemeral macroalgae, followed by fucoids and then perennial red seaweeds. After 2 years, *Chondrus crispus* had re-established approximately 50% cover on the lower shore and after 5 years it was the dominant macroalga at this height, with approximately 100% cover. The authors pointed out that although *Chondrus crispus* was a poor colonizer, it was the best competitor. Similarly MacFarlane (1952) reports that the particularly harsh winter of 1947/48 destroyed *Chondrus* beds near Pubnico. By the next summer, the annual brown alga *Chordaria* had colonized the area, and by the summer of 1950, *Fucus* had taken over as the dominant successional stage. *Chondrus* did not noticeably start to grow back in the area until summer 1951, four years later. Pringle and Semple (1980) estimated it would take about four years for a bare patch in a *Chondrus* bed to fill in with harvestable plants and five to ten years for *Chondrus* to re-establish in barren areas.

Turf forming biotopes and fucoid dominated biotopes may represent alternate stable states that continue while the dominant turf or fucoids occupy space. Removal of the turf may therefore allow re-establishment of a Fucoid or kelp dominated biotope that will remain until environmental or other factors again alter the state. Lubchenco (1980) for example, on shores in New England, found that the removal of *Chondrus crispus* turf allowed the establishment of *Fucus* spp. Removal of grazers and the turf allowed Fucus spp. to establish 100% cover, highlighting the significance of grazers in structuring the biotope. MacFarlane (1952) also recorded a shift to a *Corallina officinalis* and encrusting coralline biotope following over raking (for harvesting) of *Chondrus crispus* turf, in these areas gastropods had increased in abundance and prevented the recovery of *Chondrus crispus* by grazing. It should therefore be noted that where red algal turfs are removed, recovery may be prolonged.

Resilience assessment. Recovery rates will be greatly influenced by whether the crust stages remain from which the thalli can regrow. Where the bases remain and resistance is assessed as 'Medium' (loss of <25% of individuals or cover) or 'Low', then recovery is assessed as 'High' based on regrowth from crusts and remaining plants. Where resistance is assessed as 'Low' or 'None' and a high proportion of bases are removed then recovery may be more protracted. Based on recovery from ice scour (Minchington *et al*., (1997), biotope recovery is assessed as 'Medium' (2-10 years) where bases are removed. As recovery, where turfs are removed over large areas, will depend on the supply of propagules from neighbouring populations, and as dispersal is limited, the recovery will depend on the supply of propagules which will be influenced site-specific factors, particularly local water transport. Caveats regarding possible state shifts where beds are extensively removed should also be considered when applying sensitivity assessments. Identifying tipping points for shifts to alternate stable states is problematic, therefore although the recovery rates based on examples and life history traits are used in the assessments, these may underestimate recovery time which will be influenced by pressure and site-specific factors.

NB: The resilience and the ability to recover from human induced pressures is a combination of the environmental conditions of the site, the frequency (repeated disturbances versus a one-off event) and the intensity of the disturbance. Recovery of impacted populations will always be mediated by stochastic events and processes acting over different scales including, but not limited to, local habitat conditions, further impacts and processes such as larval-supply and recruitment between populations. Full recovery is defined as the return to the state of the habitat that existed prior to impact. This does not necessarily mean that every component species has returned to its prior

condition, abundance or extent but that the relevant functional components are present and the habitat is structurally and functionally recognizable as the initial habitat of interest. It should be noted that the recovery rates are only indicative of the recovery potential.

Hydrological Pressures

	Resistance	Resilience	Sensitivity
Temperature increase (local)	High Q: High A: High C: High	High Q: High A: High C: High	Not sensitive Q: High A: High C: High

Intertidal species are exposed to extremes of high and low air temperatures during periods of emersion. They must also be able to cope with sharp temperature fluctuations over a short period of time during the tidal cycle. In winter air temperatures are colder than the sea, conversely in summer air temperatures are much warmer than the sea. Species that occur in this intertidal biotope are therefore generally adapted to tolerate a range of temperatures.

Chondrus crispus has a wide distribution it is found extensively throughout Europe and North America records also recorded under a number of synonyms from Africa and Asia (Guiry & Guiry, 2015). Spore germination in *Chondrus crispus* appears to be temperature dependent with spores discharged at temperatures of 5°C failing to germinate although in laboratory culture at 10°C spores were viable all year round (Bhattacharya, 1985). In New Hampshire, USA, *Chondrus crispus* grows abundantly in waters with an annual variation in surface temperature from -1 to +19°C (Mathieson & Burns, 1975). The species is therefore unlikely to be particularly intolerant of temperature changes in British and Irish waters (Holt *et al.*, 1995The optimum temperature for growth has been reported as 10-15°C (Fortes & Lüning, 1980), 15°C (Bird *et al.*, 1979), 15-17°C (Tasende & Fraga, 1999) and 20°C (Simpson & Shacklock, 1979). Above the optimum temperature, growth rate is reported to decline (Bird *et al.*, 1979; Simpson & Shacklock, 1979). Compared to *Chondrus crispus* plants grown at 5°C, plants grown at 20°C had higher growth rates in terms of length, biomass, surface area, dichotomy and branch production. The differences resulted in growth of morphologically more complex thalli at higher temperatures with more efficient nutrient exchange and light harvesting (Kuebler & Dudgeon, 1996). *Chondrus crispus* plants acclimated to growth at 20°C (vs. 5°C) had higher levels of chlorophyll a and phycobilins, resulting in higher rates of light limited photosynthesis for a given photon flux density (Kuebler & Davison, 1995). Plants grown at 20°C were able to maintain constant rates of light saturated photosynthesis at 30°C for 9 hours. In contrast, in plants acclimated to 5°C, light saturated photosynthetic rates declined rapidly following exposure to 30°C (Kuebler & Davison, 1993). Prince & Kingsbury (1973) reported cessation of growth in *Chondrus crispus* cultures at 26°C, first mortality of spores at 21.1°C and total mortality of spores at 35-40°C, even if exposed for just 1 minute.

The associated *Ulva* spp. are distributed globally and occur in warmer waters than those surrounding the UK suggesting that they can withstand increases in temperature at the pressure benchmark. *Ulva* spp. are characteristic of upper shore rock pools, where water and air temperatures are greatly elevated on hot days. Empirical evidence for thermal tolerance to anthropogenic increases in temperature is provided by the effects of heated effluents on rocky shore communities in Maine, USA. *Ascophyllum* and *Fucus* were eliminated from a rocky shore heated to 27-30 °C by a power station whilst *Ulva intestinalis* (as *Enteromorpha intestinalis*)

increased significantly near the outfall (Vadas *et al*., 1976).

Barnacles (*Semibalanus balanoides*) and *Patella vulgata* occur in this biotope. Laboratory studies suggest that adults of these species can tolerate temperature increases. The median upper lethal temperature limit in laboratory tests on *Semibalanus balanoides* was approximately 35 ° (Davenport & Davenport, 2005). *Patella vulgata* can also tolerate high temperatures. The body temperature of *Patella vulgata* can exceed 36 °C in the field, (Davies, 1970); adults become non-responsive at 37-38 °C and die at temperatures of 42 °C (Evans, 1948). Although adults may be able to withstand acute and chronic increases in temperature at the pressure benchmark, increased temperatures may have sub-lethal effects on the population by impacting the success of reproduction phases. The distribution of both the key characterizing species, *Semibalanus balanoides* and *Patella vulgata* are 'northern' with their range extending from Portugal or Northern Spain to the Arctic circle. Populations in the southern part of England are therefore relatively close to the southern edge of their geographic range. Reproductive and recruitment success in both species is linked to temperature and long-term changes in temperature (exceeding the duration of the pressure benchmark) may to lead to replacement by the warm water species *Chthamalus montagui* and *Chthamalus stellatus* (Southward *et al*., 1995). In Northern Portugal warming seas appear to be linked to a shortening of the reproductive period and the lack of multiple spawning events in *Patella vulgata* and other northern species (Ribeiro *et al*., 2009).

Sensitivity assessment. Considering that maximum sea surface temperatures around the British Isles rarely exceed 20°C (Hiscock, 1998), it is unlikely that *Chondrus crispus* would suffer mortality due to the acute or chronic benchmark increase in temperature. *Mastocarpus stellatus* may be found higher on the shore and its distribution suggests that it has a higher tolerance to increased temperatures and desiccation than *Chondrus crispus*. Adults of the associated species *Patella vulgata* are considered likely to be able to tolerate an acute or chronic increase in temperature at the pressure benchmark, although the timing of acute and chronic increases would alter the degree of impact and hence sensitivity. An acute change occurring on the hottest day of the year and exceeding thermal tolerances could lead to mortality. Sensitivity of *Patella vulgata* and *Semibalanus balanoides* to longer-term, broad-scale perturbations would potentially be greater due to effects on reproduction . *Ulva* spp., are considered to tolerate increases in temperature at the pressure benchmark. Biotope resistance is therefore assessed as 'High' and recovery as 'High' (by default) so that the biotope is assessed as 'Not sensitive'.

Temperature decrease (local)	High Q: High A: High C: High	High Q: High A: High C: High	Not sensitive Q: High A: High C: High

Many intertidal species are tolerant of freezing conditions as they are exposed to extremes of low air temperatures during periods of emersion. They must also be able to cope with sharp temperature fluctuations over a short period of time during the tidal cycle. In winter air temperatures are colder than the sea, conversely in summer air temperatures are much warmer than the sea. Species that occur in the intertidal are therefore generally adapted to tolerate a range of temperatures, with the width of the thermal niche positively correlated with the height of the shore (Davenport & Davenport, 2005).

The key characterizing species, *Chondrus crispus* and *Mastocarpus stellatus* have a broad geographical distribution (Guiry & Guiry, 2015) and throughout the range experience wide variation in temperatures (although local populations may be acclimated to the prevailing thermal regime). In New Hampshire, USA, *Chondrus crispus* grows abundantly in waters with an annual

variation in surface temperature from -1 to +19°C (Mathieson & Burns, 1975). Both the key characterizing species are able to tolerate freezing although the thermal tolerances vary between these two species and are linked to the upper shore limits of these species (see changes in emergence). The photosynthetic rate of *Chondrus crispus* recovered after 3hrs at -20 °C but not after 6 hrs whereas the photosynthetic rate of *Mastocarpus stellatus* higher on the shore fully recovered from 24 hrs at -20 °C (Dudgeon *et al.* (1989). Photosynthesis in *Mastocarpus stellatus* also recovered more quickly after experimental freezing (Dudgeon et al., 1989, 1995). Frond bleaching and declines in photosynthesis and growth also occur in long-term experimental exposure to periodic freezing in *Chondrus crispus* (Dudgeon *et al*., 1990). Plants from Maine, USA, were frozen at -5°C for 3 hours a day for 30 days. Photosynthesis was reduced to 55% of control values, growth rates were reduced and fronds were eventually bleached and fragmented resulting in biomass losses. Additionally, fronds of *Chondrus crispus* which were frozen daily had higher photosynthetic rates following subsequent freezing events than unfrozen controls, indicating that the species is able to acclimate to freezing conditions (Dudgeon *et al.*, 1990). *Mastocarpus stellatus* were also subjected to a similar periodic freezing regime (3 hours/day at -5°C for 36 days) with no effect on photosynthesis or growth.

Spore germination in *Chondrus crispus* appears to be temperature dependent with spores discharged at temperatures of 5°C failing to germinate although in laboratory culture at 10°C spores were viable all year round (Bhattacharya, 1985). Acute or chronic changes in temperature below 5°C may therefore reduce reproductive success although reproduction and vegetative growth in warmer months should compensate for any reduction in output.

Other species associated with the biotope are able to tolerate decreases in temperature. Lüning (1990) reported that *Corallina officinalis* from Helgoland survived 0 °C when exposed for one week. New Zealand specimens were found to tolerate -4 °C (Frazer *et al*., 1988). *Ulva* spp. are eurytopic, found in a wide temperature range and in areas which frequently experience freezing conditions and are vulnerable to ice scour (Seed & Suchanek 1992).

The limpet *Patella vulgata* and the barnacle *Semibalanus balanoides* are both northern species and relatively close to their southern range limit in the UK, suggesting these are tolerant of colder temperatures than those typically experienced in UK habitats. The tolerance of *Semibalanus balanoides*, collected in the winter (and thus acclimated to lower temperatures), to low temperatures was tested in the laboratory. The median lower lethal temperature tolerance was -14.6 °C (Davenport & Davenport, 2005). A decrease in temperature at the pressure benchmark is therefore unlikely to negatively affect this species. Adults of *Patella vulgata* are also largely unaffected by short periods of extreme cold. Ekaratne & Crisp (1984) found adult limpets continuing to grow over winter when temperatures fell to -6 °C, and stopped only by still more severe weather. Loss of adhesion after exposure to -13 °C has been observed with limpets falling off rocks and therefore becoming easy prey to crabs or birds (Fretter & Graham, 1994). However, in the very cold winter of 1962-3 when temperatures repeatedly fell below 0 °C over a period of 2 months large numbers of *Patella vulgata* were found dead (Crisp, 1964). Periods of frost may also kill juvenile *Patella vulgata*, resulting in recruitment failures in some years (Bowman & Lewis, 1977).

In colder conditions an active migration by mobile species found within the turf may occur down the shore to a zone where exposure time to the air (and hence time in freezing temperatures) is less.

Sensitivity assessment. Both the key characterizing species, *Chondrus crispus* and *Mastocarpus stellatus*, occur over a wide geographical range and as intertidal species are predicted to have high

tolerances for decreased temperature at the acute and chronic pressure benchmarks. Laboratory experiments indicate that both species are able to tolerate periodic freezing (Dudgeon *et al.*, 1995). However, reduced temperatures would probably result in suboptimal growth and may affect reproduction. Biotope resistance is assessed as 'High' as these effects do not result in mortality and resilience is assessed as 'High', so that the biotope is not considered to be sensitive to this pressure. The timing of changes and seasonal weather could result in greater impacts on species. An acute decrease in temperature coinciding with unusually low winter temperatures may exceed thermal tolerances and lead to mortalities of the associated species although this would not alter the character of the biotope.

Salinity increase (local)	High Q: High A: Low C: High	High Q: High A: High C: High	Not sensitive Q: High A: Low C: High

This biotope occurs in full salinity (30-35 ppt). Connor *et al.*, (2004). Biotopes found in the intertidal will naturally experience fluctuations in salinity where evaporation increases salinity and inputs of rainwater expose individuals to freshwater. Species found in the intertidal are therefore likely to have some form of behavioural or physiological adaptations to changes in salinity.

More evidence was found to assess *Chondrus crispus* than *Mastocarpus stellatus*. *Chondrus crispus* is found in a range of salinities across its range and has been reported from sites with yearly salinity range 0-10 psu and 10-35 psu (Lindgren & Åberg 1996) and sites from an average of 26-32 psu. However, at different salinities the ratio between the abundance of the tetrasporophyte phase and the gametophyte alters (Guido & Grace, 2010). Mathieson & Burns (1971) recorded maximum photosynthesis of *Chondrus crispus* in culture at 24 psu, but rates were comparable at 8, 16 and 32 psu. Photosynthesis continued up to 60 PSU. Bird *et al.* (1979) recorded growth of Canadian *Chondrus crispus* in culture between 10 and 50 psu, with a maximum at 30 psu. *Chondrus crispus* would therefore appear to be euryhaline and tolerant of a range of salinities.

The associated *Ulva* species can survive hypersaline conditions in supralittoral rockpools subjected to evaporation and are considered to be a very euryhaline, tolerant of extreme salinities ranging from 0 psu to 136 psu (Reed & Russell, 1979). Some variations in salinity tolerance between populations of *Ulva intestinalis* have been found, however, suggesting that plants have some adaptation to the local salinity regime (Alström-Rapaport *et al.*, 2010; Reed & Russell (1979). Increased salinity is most likely to occur in the region of the littoral fringe and supralittoral zone and specimens from these areas were able to tolerate very high salinities, a significant decrease in regeneration only being recorded after exposure to concentrated seawater (102 psu and 136 psu) for > 7 days (Reed & Russell, 1979). In the laboratory, *Semibalanus balanoides* was found to tolerate salinities between 12 and 50 psu (Foster, 1970). Young *Littorina littorea* inhabit rock pools where salinity may increase above 35psu.

Sensitivity assessment. No specific evidence was found for the salinity tolerance of *Mastocarpus stellatus*. If *Chondrus crispus* has the greater tolerance for increased salinity a change at the pressure benchmark may lead to increased dominance of the turf by that species. An increase at the pressure benchmark may also lead to an increase in abundance of the very euryhaline *Ulva* spp. Based on the salinity tolerances of *Chondrus crispus* an increase at the pressure benchmark may lead to some changes in the composition of the algal turf but not alter it from the biotope description. Resistance (of the biotope) is therefore assessed as 'High;' and resilience as 'High' (by default), and the biotope is assessed as 'Not sensitive'.

Salinity decrease (local)	High Q: High A: High C: High	High Q: High A: High C: High	Not sensitive Q: High A: High C: High

Biotopes found in the intertidal will naturally experience fluctuations in salinity where evaporation increases salinity and inputs of rainwater expose individuals to freshwater. Species found in the intertidal are therefore likely to have some form of behavioural or physiological adaptations to changes in salinity. As this biotope is present in full salinity (30-35 ppt, Connor *et al*., 2004), the assessed change at the pressure benchmark is a reduction in salinity to a variable regime (18-35 ppt) or reduced regime (18-30 ppt).

Chondrus crispus does occur in areas of 'low' salinity. For example, the species occurs in estuaries in New Hampshire, USA, where surface water salinity varies from 16-32 psu (Mathieson & Burns, 1975). Mathieson & Burns (1971) recorded maximum photosynthesis of *Chondrus crispus* in culture at 24 psu, but rates were comparable at 8, 16 and 32 psu. Tasende & Fraga (1999) cultured *Chondrus crispus* spores from north west Spain and concluded that growth was correlated with salinity between 23 and 33 psu. A reduction in salinity, therefore, is unlikely to result in mortality of *Chondrus crispus* but may suppress growth.

Sensitivity assessment. No specific evidence was found for the salinity tolerance of *Mastocarpus stellatus*. If *Chondrus crispus* has the greater tolerance for reduced salinity a change at the pressure benchmark may lead to increased dominance of the turf by that species. An increase at the pressure benchmark may also lead to an increase in abundance of the very euryhaline *Ulva* spp. Based on the salinity tolerances of *Chondrus crispus* a decrease in salinity at the pressure benchmark may lead to some changes in the composition of the algal turf but not alter it from the biotope description. Resistance (of the biotope) is therefore assessed as 'High;' and resilience as 'High' (by default), and the biotope is assessed as 'Not sensitive'.

Water flow (tidal current) changes (local)	High Q: High A: High C: High	High Q: High A: High C: High	Not sensitive Q: High A: High C: High

As water velocity increases *Mastocarpus stellatus* and *Chondrus crispus* can flex and reconfigure to reduce the size of the alga when aligned with the direction of flow, this minimises drag and hence the risk of dislodgement (Boller & Carrington, 2007). These characteristics allow these species to persist on shores that experience a range of flow speeds. For example, *Chondrus crispus* and *Mastocarpus stellatus* occur at sites in Maine, USA experiencing peak Autumn flow speeds as measured by current meters of 9.2 m/s and 5.8 m/s. At the more exposed sites with higher flow speeds some *Chondrus crispus* were dislodged during the winter. Biogenic habitat structures reduce the effects of water flows on individuals by slowing and disrupting flow. Boller and Carrington (2006) found that the canopy created by a turf of *Chondrus cripsus* reduced drag forces on individual plants by 15-65%.

Sensitivity assessment. As the key characterizing species *Chondrus crispus* and *Mastocarpus stellatus* can occur in a range of flow speeds and flex to reduce drag, resistance of the biotope was assessed as 'High', resilience was assessed as 'High' (by default), so that the biotope is classed as 'Not sensitive'.

Emergence regime changes	Low Q: High A: Low C: Medium	Medium Q: High A: Low C: Medium	Medium Q: High A: Low C: Medium

Emergence regime is a key factor structuring this (and other) intertidal biotopes. This biotope generally occurs in the lower eulittoral above the main kelp zone, stands of *Alaria esculenta* or the mussel, *Mytilus edulis* (Connor *et al*., 2004). In general red algae can tolerate low levels and can extend into the subtidal. However, decreased emergence would be likely to lead to the establishment of kelps and Alaria esculenta and would alter the character of the biotope from the description.

Studies have demonstrated that *Chondrus crispus* is more sensitivie to freezing and desiccation than *Mastocarpus stellatus* (Mathieson & Burns, 1971; Dudgeon *et al*., 1989) which probably limits the height on which it grows on the shore. *Chondrus crispus* is therefore more likely to be sensitive than *Mastocarpus stellatus* to increased emergence although desiccation rather than temperature may exert a greater control where winter temperatures are higher. A study by Lubchenco (1980) on the coast of New England suggested that desiccation is an important factor determining the upper limit of *Chondrus crispus*. The species was found to extend into the mid-intertidal where it was found underneath a fucoid canopy. Removal of this canopy lead to bleached, dried out and dead plants within two to three weeks (Lubchenco, 1980). Hawkins & Hartnoll (1985) also observed bleaching of red algae species including *Chondus crispus* and *Mastocarpus* (as *Gigartina*) *stellata*, during an unusually hot summer. The loss of canopy forming alae exacerbated the impact.

An increase in emergence will also increase the exposure of *Chondrus crispus* to solar radiation. *Chondrus crispus* is growth saturated at light levels of 60-70 µE/m/s and is not photoinhibited at 250 µE/m/s (Bird *et al*., 1979; Fortes & Lüning, 1980). However, Bischoff *et al*. (2000) reported that the photochemistry of *Chondrus crispus* is negatively affected by UV-B radiation, while Aguirre-von-Wobeser *et al*. (2000) concluded that photosynthetically active radiation (PAR) is responsible for most of the photoinhibition in the species. Bischof *et al*. (2000) suggested that intolerance to UV-B may be a factor restricting *Chondrus crispus* to the subtidal and lower intertidal, whereas *Mastocarpus stellatus*, which is better adapted to UV radiation, competes better at higher shore levels.

Increased emergence may reduce habitat suitability for the associated species, although ephemeral green algae, *Patella vulgata*, *Semibalanus balanoides* and littorinids are found at a range of shore levels and are found in abundance at higher shore levels than this biotope typically occurs at. These species are therefore considered not to be affected by increased emergence.
Experimental grazer removal has allowed algae including *Palmaria palmata*, *Ceramium* sp. and *Osmundea* (as *Laurencia*) *pinnatifida* to grow higher on the shore (during winter and damp summers) than usual suggesting that grazing also limits the upper shore extent of this biotope. An increase in grazers and grazing within this biotope associated with reduced predation level by crabs and predators following increased emergence may removal algae but grazing on the characterizing, mature red algae turf is probably limited and may serve to check the growth of green algae. A significant, long-term, increase in emergence is therefore likely to lead to replacement of this biotope with one more typical of the changed conditions dominated by limpets, barnacles and fucoids for example.

Sensitivity assessment. Significant long-term changes in emergence would result in changes in environmental factors and grazing pressures and lead to increased competition from species better adapted to the changed conditions. Resistance to this pressure is therefore assessed as 'Low'. Resilience is assessed as 'Medium' (where bases are removed) and sensitivity to this

pressure is assessed as ‘Medium’.

Wave exposure changes (local)	High Q: High A: Medium C: High	High Q: High A: High C: High	Not sensitive Q: High A: Medium C: High

This biotope is recorded from locations that are judged to range from moderately exposed or exposed (Connor *et al*., 2004). The degree of wave exposure influences wave height, as in more exposed areas with a longer fetch waves would be predicted to be higher. As this biotope occurs across a range of exposures, this was therefore considered to indicate, by proxy, that biotopes in the middle of the wave exposure range would tolerate either an increase or decrease in significant wave height at the pressure benchmark.

Chondrus crispus typically occurs in 'sheltered' and 'moderately exposed areas' (Dixon & Irvine, 1977). Strong wave action is likely to cause some damage to fronds of both the key characterizing species resulting in reduced photosynthesis and compromised growth. Furthermore, individuals may be damaged or dislodged by scouring from sand and gravel mobilized by increased wave action (Hiscock, 1983). Dudgeon & Johnson (1992) noted wave induced disturbance of intertidal *Chondrus crispus* on shores of the Gulf of Maine during winter where 25-30% of cover of large *Chondrus crispus* thalli was lost in one winter. *Chondrus crispus* suffers greater losses than *Mastocarpus stellatus* in areas of increased wave action as the drag forces on the thallus are greater for the larger and bushier plants (Dudgeon & Johnson, 1992; Pratt & Johnson, 2002). Greater dislodgement of the faster growing *Chondrus crispus* by wave action during winter storms is a factor mediating competition between the two key characterizing species (Pratt & Johnson, 2002).

Gutierrez & Fernandez (1992) described morphological variability of *Chondrus crispus* according to wave exposure and emersion. They identified 2 well defined morphotypes; filiform and planiform. The filiform morphotype had fewer dichotomies per unit length, a circular cross section, narrow fronds and was abundant in the low intertidal and at more exposed sites. The planiform morphotype had more dichotomies, was smaller, with a flattened cross section, broader fronds and was abundant higher up the shore and in more sheltered areas. An increase or decrease in wave exposure greater than the pressure benchmark may therefore lead to shifts between the filiform and planiform morphyotypes.

A decrease in wave exposure at the pressure benchmark is unlikely to affect *Chondrus crispus* or *Mastocarpus stellatus* directly. Decreases greater than the pressure benchmark that lead to changes in suspended solids and subsequent deposition may lead to changes in the assemblage (see siltation and changes in suspended sediment pressures).

Sensitivity assessment. The biotope is found across a range of wave exposures, mid-range populations are considered to have 'High' resistance to a change in significant wave height at the pressure benchmark. Resilience is assessed as ‘High’, by default, and the biotope is considered ‘Not sensitive’.

Chemical Pressures

	Resistance	Resilience	Sensitivity
Transition elements & organo-metal contamination	Not Assessed (NA) Q: NR A: NR C: NR	Not assessed (NA) Q: NR A: NR C: NR	Not assessed (NA) Q: NR A: NR C: NR

This pressure is **Not assessed** but evidence is presented where available.

Contamination by non-synthetic chemicals, at levels greater than the pressure benchmark may adversely impact the biotope. Little information was found concerning the intolerance of *Chondrus crispus* to heavy metals. Burdin & Bird (1994) reported that both gametophyte and tetrasporophyte forms accumulated Cu, Cd, Ni, Zn, Mn and Pb when immersed in 0.5 mg/l solutions for 24 hours. No effects were reported however, and no relationship was detected between hydrocolloid characteristics and heavy metal accumulation. Bryan (1984) suggested that the general order for heavy metal toxicity in seaweeds is: Organic Hg > inorganic Hg > Cu > Ag > Zn > Cd > Pb. Cole *et al.* (1999) reported that Hg was very toxic to macrophytes. The sub-lethal effects of Hg (organic and inorganic) on the sporelings of an intertidal red algae, *Plumaria elegans*, were reported by Boney (1971). 100% growth inhibition was caused by 1 ppm Hg. In light of the lack of information found, an intolerance assessment has not been attempted.

Hydrocarbon & PAH contamination	Not Assessed (NA) Q: NR A: NR C: NR	Not assessed (NA) Q: NR A: NR C: NR	Not assessed (NA) Q: NR A: NR C: NR

This pressure is **Not assessed** but evidence is presented where available

Contamination at levels greater than the pressure benchmark may adversely impact the biotope. The long-term effects on *Chondrus crispus* of continuous doses of the water accommodated fraction (WAF) of diesel oil were determined in experimental mesocosms (Bokn *et al.*, 1993). Mean hydrocarbon concentrations tested were 30.1 µg/l and 129.4 µg/l. After 2 years, there were no demonstrable differences in the abundance patterns of *Chondrus crispus*. Kaas (1980) (cited in Holt *et al.*, 1995) reported that the reproduction of adult *Chondrus crispus* plants on the French coast was normal following the *Amoco Cadiz* oil spill. However, it was suggested that the development of young stages to adult plants was slow, with biomass still reduced 2 years after the event. O'Brien & Dixon (1976) and Grandy (1984) (cited in Holt *et al.*, 1995) comment on the high intolerance of red algae to oil/dispersant mixtures, but it is unclear which factor is responsible for the intolerance.

Synthetic compound contamination	Not Assessed (NA) Q: NR A: NR C: NR	Not assessed (NA) Q: NR A: NR C: NR	Not assessed (NA) Q: NR A: NR C: NR

This pressure is **Not assessed** but evidence is presented where available.

Contamination at levels greater than the pressure benchmark may adversely impact the biotope. No evidence was found specifically relating to the intolerance of *Chondrus crispus* to synthetic chemicals. However, inferences may be drawn from the sensitivities of red algal species generally. O'Brien & Dixon (1976) suggested that red algae were the most sensitive group of algae to oil or dispersant contamination, possibly due to the susceptibility of phycoerythrins to destruction. They also report that red algae are effective indicators of detergent damage since they undergo colour changes when exposed to relatively low concentration of detergent. Smith (1968) reported that 10 ppm of the detergent BP 1002 killed the majority of specimens in 24hrs in toxicity tests, although *Chondrus crispus* was amongst the algal species least affected by the detergent used to clean up the *Torrey Canyon* oil spill. Laboratory studies of the effects of oil and dispersants on several red algal species concluded that they were all sensitive to oil/dispersant mixtures, with little difference between adults, sporelings, diploid or haploid life stages (Grandy, 1984, cited in Holt *et al.*, 1995). Cole *et al.* (1999) suggested that herbicides, such as simazine and atrazine, were very toxic to macrophytes. The evidence suggests that in general red algae are very sensitive to synthetic

chemicals. Intolerance of *Chondrus crispus* is therefore recorded as high. Recoverability is recorded as high (see additional information below) although it may take up to 5 years as recovery will be largely dependent on recruitment of spores from distant unperturbed populations.

Radionuclide contamination	No evidence (NEv) Q: NR A: NR C: NR	Not relevant (NR) Q: NR A: NR C: NR	No evidence (NEv) Q: NR A: NR C: NR

No evidence was found to assess this pressure at the benchmark. Algae bioaccumulate radionuclides (with extent depending on the radionuclide and the algae species). A study in France found that *Chondrus crispus* was capable of absorbing a large number of artificial radioactive elements and that this had consequences considering the exploitation of this species as a harvestable resource (Cosson *et al*., 1984). However, no information was found concerning the actual effects of radionuclide on *Chondrus crispus*. Adverse effects have not been reported at low levels.

Introduction of other substances	Not Assessed (NA) Q: NR A: NR C: NR	Not assessed (NA) Q: NR A: NR C: NR	Not assessed (NA) Q: NR A: NR C: NR

This pressure is **Not assessed**.

De-oxygenation	High Q: Low A: NR C: NR	High Q: High A: High C: High	Not sensitive Q: Low A: Low C: Low

The effects of reduced oxygenation on algae are not well studied. Plants require oxygen for respiration, but this may be provided by production of oxygen during periods of photosynthesis. Lack of oxygen may impair both respiration and photosynthesis (see review by Vidaver, 1972). A study of the effects of anoxia on another red alga, *Delesseria sanguinea*, revealed that specimens died after 24 hours at 15°C but that some survived at 5°C (Hammer, 1972). This biotope would only be exposed to low oxygen in the water column intermittently during periods of tidal immersion. In addition, in areas of wave exposure and moderately strong current flow low oxygen levels in the water are unlikely to persist for very long as oxygen levels will be recharged by the incorporation of oxygen in the air into the water column or flushing with oxygenated waters.

No evidence was found to assess this pressure for the red algae turfs. However, the associated species are unlikely to be impacted by this pressure, at the benchmark. Experiments have shown that thallus discs of *Ulva lactuca* plants can survive prolonged exposure to anoxia and hypoxia (Vermaat & Sand-Jensen, 1987; Corradi *et al*., 2006). Following resumption of normal oxygen conditions gametes were produced. The associated invertebrate species also show high tolerances for reduced oxygen at levels that exceed the pressure benchmark. *Littorina littorea* can easily survive 3-6 days of anoxia (Storey *et al*., 2013). *Semibalanus balanoides* can respire anaerobically, so they can tolerate some reduction in oxygen concentration (Newell, 1979). When placed in wet nitrogen, where oxygen stress is maximal and desiccation stress is low, *Semibalanus balanoides* have a mean survival time of 5 days (Barnes *et al*., 1963). Limpets can also survive for a short time in anoxic seawater; Grenon & Walker, (1981) found that in oxygen free water limpets could survive up to 36 hours, although Marshall & McQuaid (1989) found a lower tolerance for *Patella granularis*, which survived up to 11 hours in anoxic water. *Patella vulgata* and *Littorina littorea* are able to respire in air, mitigating the effects of this pressure during the tidal cycle.

Sensitivity assessment. No direct evidence for the effects of hypoxia on red algal turfs was found. As the biotope will only be exposed to this pressure when emersed and respiration will occur in air, biotope resistance was assessed as 'High' and resilience as 'High' (no effect to recover from), resulting in a sensitivity of 'Not sensitive'.

Nutrient enrichment	High Q: High A: High C: High	High Q: High A: High C: High	Not sensitive Q: High A: High C: High

In studies of *Chondrus crispus* from Prince Edward Island, Canada, Juanes & McLachlan (1992) concluded that primary production was limited by temperature during the autumn to spring period and by nitrogen availability when production was maximal in the summer. They suggested that growth of *Chondrus crispus* became nutrient limited at approximately 14°C. To a certain degree, therefore, an increase in the level of nutrients would be likely to enhance growth of *Chondrus crispus*.

However, if nutrient enrichment is extended or prolonged, *Chondrus crispus* may be out-competed by faster growing or ephemeral species. Johansson *et al.* (1998) investigated the changes in the algal vegetation of the Swedish Skagerrak coast, an area heavily affected by eutrophication, between 1960 and 1997. Slow growing species, including *Chondrus crispus* declined in abundance, probably due to competition from faster growing red algal species such as *Phycodrys rubens* and *Delesseria sanguinea*.

Atalah & Crowe (2010) added nutrients to rockpools. The rockpools were occupied by a range of algae including encrusting corallines, turfs of *Mastocarpus stellatus*, *Chondrus crispus* and *Corallina officinalis* and green and red filamentous algae. Nitrogen and phosphorous enhancement was via the addition of fertilisers, as either 40 g/litre or 20 g/litre. The treatments were applied for seven months and experimental conditions were maintained every two weeks. The experimental treatments do not directly relate to the pressure benchmark but indicate some general trends in sensitivity. Nutrients had no significant effect on the cover of crustose coralline algae or the cover of red turfing algae. However, the cover of green filamentous algae increased where grazers were removed (Atalah & Crowe, 2010).

The study and Atalah & Crowe (2010) suggests that, although red algal turfs may be tolerant of eutrophication and may even benefit biotope composition may alter due to the proliferation of fast growing ephemeral algae.

Sensitivity assessment. The pressure benchmark is set at a level that is relatively protective and based on the evidence and considerations outlined above the biological assemblage is considered to be 'Not sensitive' at the pressure benchmark. Resistance and resilience are therefore assessed as 'High'.

Organic enrichment	High Q: Low A: NR C: NR	High Q: High A: High C: High	Not sensitive Q: High A: High C: High

No evidence was found to assess this pressure. The biotope is considered to be structured largely by wave exposure and the presence of algal turfs rather than food supply. Additional organic matter supplied to this biotope is likely to be removed by wave action or trapped and incorporated into the sediment mat associated with the algal turf. Within the mat it would enhance secondary production by the associated polychaetes and amphipods and would be likely to be rapidly

consumed. Resistance to this pressure is therefore assessed as 'High' and resilience as 'High' and the biotope is considered to be 'Not sensitive'.

Physical Pressures

	Resistance	Resilience	Sensitivity
Physical loss (to land or freshwater habitat)	None Q: High A: High C: High	Very Low Q: High A: High C: High	High Q: High A: High C: High

All marine habitats and benthic species are considered to have a resistance of 'None' to this pressure and to be unable to recover from a permanent loss of habitat (resilience is 'Very Low'). Sensitivity within the direct spatial footprint of this pressure is therefore 'High'. Although no specific evidence is described confidence in this assessment is 'High', due to the incontrovertible nature of this pressure.

Physical change (to another seabed type)	None Q: High A: High C: High	Very Low Q: High A: High C: High	High Q: High A: High C: High

The loss of hard substratum would remove the rock habitat and sediments would be unsuitable for *Mastocarpus stellatus* and *Chondrus crispus* and other attached algae that characterize this biotope. Other associated species such as barnacles and limpets and spirorbid polychaetes would be lost as these are associated with hard surfaces rather than sedimentary habitats.

Artificial hard substratum may also differ in character from natural hard substratum, so that replacement of natural surfaces with artificial may lead to changes in the biotope through changes in species composition, richness and diversity (Green *et al*., 2012; Firth *et al*., 2013) or the presence of non-native species (Bulleri & Airoldi, 2005). *Chondrus crispus* readily colonised artificial settlement plates and by the end of the experiment was the dominant species on plates (Harlin & Lindbergh, 1977). *Chondrus crispus* were however significantly more abundant on the substratum with the largest particles (1-2 mm) and only a few individuals were found on the smooth surface, demonstrating that artificial smooth surfaces may not provide an optimal habitat.

Sensitivity assessment. Based on the loss of suitable habitat resistance is assessed as 'None' recovery is assessed as 'Very Low' as the change at the pressure benchmark is permanent. Sensitivity is therefore 'High'.

Physical change (to another sediment type)	Not relevant (NR) Q: NR A: NR C: NR	Not relevant (NR) Q: NR A: NR C: NR	Not relevant (NR) Q: NR A: NR C: NR

Not relevant to biotopes occurring on bedrock.

Habitat structure changes - removal of substratum (extraction)	Not relevant (NR) Q: NR A: NR C: NR	Not relevant (NR) Q: NR A: NR C: NR	Not relevant (NR) Q: NR A: NR C: NR

The species characterizing this biotope are epiflora and epifauna occurring on rock and would be sensitive to the removal of the habitat. However, extraction of rock substratum is considered

unlikely and this pressure is considered to be 'Not relevant' to hard substratum habitats.

Abrasion/disturbance of the surface of the substratum or seabed	Medium Q: High A: Low C: NR	High Q: High A: High C: High	Low Q: High A: Low C: Low

Little information is available on the effects of abrasion on intertidal red algae. Brosnan & Crumrine (1994) noted that trampling significantly reduced algal cover within 1 month of trampling. Foliose algae were particularly affected and decreased in cover from 75% to 9.1% in trampled plots. *Mastocarpus papillatus* decreased in abundance from 9% to 1% in trampled plots but increased in control plots.

Sensitivity assessment. The impact of surface abrasion will depend on the footprint, duration and magnitude of the pressure. Biotope resistance, to a single abrasion event is assessed as 'Medium' (<25% of population damaged or removed), as some damage may occur and some fronds may be removed although the bases may remain. Resilience is assessed as 'High', (through regrowth of fronds), so that biotope sensitivity is assessed as 'Low'. Resistance and resilience will be lower (and hence sensitivity greater) to abrasion events that exert a greater crushing force and remove the bases, or that occur at greater intensities and duration.

Penetration or disturbance of the substratum subsurface	Not relevant (NR) Q: NR A: NR C: NR	Not relevant (NR) Q: NR A: NR C: NR	Not relevant (NR) Q: NR A: NR C: NR

The species characterizing this biotope group are epiflora and epifauna occurring on rock which is resistant to subsurface penetration. The assessment for abrasion at the surface only is therefore considered to equally represent sensitivity to this pressure.

Changes in suspended solids (water clarity)	High Q: Low A: NR C: NR	High Q: High A: High C: High	Not sensitive Q: Low A: Low C: Low

No empirical evidence was found to assess this pressure. Intertidal biotopes will only be exposed to this pressure when submerged during the tidal cycle and thus have limited exposure. Siltation, which may be associated with increased suspended solids is assessed separately. As photoautotrophs, the key characterizing red algal turf species *Mastocarpus stellatus and Chondrus crispus* are likely to benefit from reduced turbidity, as the light attenuating effects of turbid water reduce photosynthesis. As these species can occur subtidally the limited shading from suspended solids during immersion is not considered to negatively affect the red algal turf. Suspended sediments may have abrading effects on the fronds. However *as* turfs of red algae trap sediments they clearly have some tolerance for abrasion and scour. *Chondrus crispus* occurs in areas of sand covered rock in the subtidal biotope IR.HIR.KSed.ProtAhn suggesting it is very resistant to high levels of turbidity and scour associated with high levels of resuspended particles. An increase in suspended solids above the pressure benchmark may result in a change in species composition with an increase in species seen in very turbid, silty environments e.g. *Ahnfeltia plicata*, *Rhodothamniella floridula*, *Polyides rotunda* and *Furcellaria lumbricalis*.

Sensitivity assessment. The exposure of this biotope to suspended solids in the water column will be limited to immersion periods. The biotope is considered to be 'Not sensitive' to a reduction in suspended solids. An increase in suspended solids may lead to some sub-lethal abrasion of fronds but this will be compensated by the high growth rates exhibited by the characterizing species. Resistance is therefore assessed as 'High' and resilience as 'High' (by default) so that the biotope is considered to be 'Not sensitive'.

Smothering and siltation rate changes (light)	Medium Q: High A: Low C: Medium	High Q: High A: Low C: Medium	Low Q: High A: Low C: Medium

Sedimentation can directly affect assemblages inhabiting rocky shores through burial/smothering and scour/abrasion of organisms. This biotope occurs low on the shore, in moderately exposed conditions. In areas experiencing wave action, excess sediments are likely to be removed from the rock surface within a few tidal cycles, reducing the time of exposure to this pressure.

The state of the tide will mediate the degree of impact on macroalgae. If smothering occurs at low tide when the algae is lying flat on the substratum, then most of the organism as well as the associated community will be covered by the deposition of fine material at the level of the benchmark. Smothering will prevent photosynthesis resulting in reduced growth and eventually death. If however smothering occurs whilst the alga is submerged standing upright then some of the photosynthetic surfaces of adult plants may be left uncovered. The resistance of this biotope to the given pressure may therefore vary with time of day.

Recently settled propagules, regenerating holdfasts and small developing plants would be buried by 5 cm of sediment and be unable to photosynthesize. For example, Vadas *et al.* (1992) stated that algal spores and propagules are adversely affected by a layer of sediment, which can exclude up to 98% of light.

Other species within the biotope, particularly limpets and littorinids are considered more sensitive to sedimentation. Chandrasekara & Frid (1998) specifically tested the siltation tolerance of *Littorina littorea*. Approximately half of the test individuals could not regain the surface from 1cm of burial except in the most favourable conditions (low temperatures, high water, high silt when a majority (10 out of 15) of the test cohort surfaced. Field observations support the findings that *Littorina littorea* are generally unable to survive smothering. Albrecht & Reise (1994) observed a population of *Littorina littorea* in a sandy bay near the Sylt island in the North Sea. They found that the accretion of mud within *Fucus* strands and subsequent covering of *Littorina* by the sediment resulted in them suffocating and a significant reduction in their abundance. Field observations and laboratory experiments have highlighted the sensitivity of limpets to sediment deposition Airoldi & Hawkins (2007) tested the effects of different grain sizes and deposit thickness in laboratory experiments using *Patella vulgata*. At 1 and 2 mm thicknesses, fine sediments decreased grazing by 40 and 77 %. The addition of approximately 4 mm of fine sediment completely inhibited grazing. Limpets tried to escape the sediment but lost attachment and died after a few days (Airoldi & Hawkins, 2007) Observations on exposed and sheltered shores with patches of sediment around Plymouth in the south west of England confirmed that *Patella vulgata* abundances were higher where deposits were absent. The limpets were locally absent in plots with 50-65% sediment cover (Airoldi & Hawkins, 2007).

Atalah & Crowe (2010) added sediment to rockpools. The rockpools were occupied by a range of algae including encrusting corallines and turfs of *Mastocarpus stellatus*, *Chondrus crispus* and *Corallina officinalis* and green and red filamentous algae. Sediment treatment involved the addition

of a mixture of coarse and fine sand of either 300 mg/cm^2/month or 600 mg/cm^2 every 15 days. The treatments were applied for seven months and experimental conditions were maintained every two weeks. The experimental treatments do not directly relate to the pressure benchmark but indicate some general trends in sensitivity. Sedimentation led to an increase in the mean cover of red turfing algae (*Mastocarpus stellatus* and *Chondrus crispus* and *Corallina officinalis*) from 11.7% (±1.0 S.E.) in controls to 26.1% (±4.7 S.E.) in sedimented assemblages, but there were no differences between the two levels of sedimentation (Atalah & Crowe, 2010).

Sensitivity assessment. Deposition of 5 cm of fine material (see benchmark) in a single incident may lower survival and germination rates of spores and cause some mortality in early life stages of the red algae within the biotope. Adults are more resistant but will experience a decrease in growth and photosynthetic rates. Mortality will be more limited, and possibly avoided, where the smothering sediment is removed due to wave action or tidal streams, depending on how long the sediment remains. Biotope resistance is assessed as 'Medium' and resilience is assessed as 'High' (based on regrowth from holdfasts). So that biotope sensitivity is judged to be 'Low'. It should be noted that the associated *Patella vulgata* may have higher sensitivity to this pressure.

Smothering and siltation rate changes (heavy)	Low Q: Low A: NR C: NR	High Q: High A: Low C: Medium	Low Q: Low A: Low C: Low

No evidence was found to assess this pressure at the benchmark. Sensitivity to this pressure will be mediated by site-specific hydrodynamic conditions and the footprint of the impact. A deposit at the pressure benchmark would cover species with a thick layer of fine materials, however, as this biotope occurs in the lower intertidal on wave exposed shores it is subject to prolonged immersion and silts may be relatively rapidly re-suspended and removed. Where a large area is covered sediments may be shifted by wave and tides rather than removed.

Mortality of red algae is likely to depend on the duration of smothering, where wave action rapidly mobilises and removes fine sediments, survival may be much greater.

Species associated with this biotope such as limpets would not be able to escape from deposits and would likely suffer mortality (see evidence for light siltation). Even the most tolerant of organisms would eventually suffer from inhibition and mortality following smothering although the thresholds for these effects have has not been identified (Airoldi, 2003).

The evidence for siltation effects on the associated species, *Patella vulgata*, are outlined above for 'light' deposition. In summary, experiments by Airoldi & Hawkins (2007), supported by field observations, indicate that this species would be unable to escape from sediment deposits of 30cm thickness and would rapidly die.

Sensitivity assessment. At the level of the benchmark (30 cm of fine material added to the seabed in a single event), smothering is likely to result in death and removal of red algal fronds, germlings and invertebrate grazers and biotope resistance is assessed as 'Low'. Resilience is assessed as 'High' (based on survival of holdfasts). Overall the biotope has a 'Low' sensitivity to siltation at the pressure benchmark, based on recovery of *Palmaria palmata* via re-growth from holdfasts.

Litter	Not Assessed (NA) Q: NR A: NR C: NR	Not assessed (NA) Q: NR A: NR C: NR	Not assessed (NA) Q: NR A: NR C: NR

Not assessed.

Electromagnetic changes	No evidence (NEv) Q: NR A: NR C: NR	No evidence (NEv) Q: NR A: NR C: NR	No evidence (NEv) Q: NR A: NR C: NR

No evidence.

Underwater noise changes	Not relevant (NR) Q: NR A: NR C: NR	Not relevant (NR) Q: NR A: NR C: NR	Not relevant (NR) Q: NR A: NR C: NR

Not relevant.

Introduction of light or shading	High Q: High A: Low C: Medium	High Q: High A: High C: High	Not sensitive Q: High A: Low C: Medium

Canopy removal experiments in a rocky sub tidal habitat in Nova Scotia, Canada by Schmidt & Scheibling (2007) did not find a shift in understorey macraoalgal turfs (dominated by *Corallina officinalis*, *Chondrus crispus* and *Mastocarpus stellatus*) to more light-adapted species over 18 months.

Chondrus crispus is growth saturated at light levels of 60-70 µE/m²/s and is not photoinhibited at 250 µE/m²/s (Bird *et al*., 1979; Fortes & Lüning, 1980). However, Bischof *et al*. (2000) reported that the photochemistry of *Chondrus crispus* is negatively affected by UV-B radiation, while Aguirre-von-Wobeser *et al*. (2000) concluded that photosynthetically active radiation (PAR) is responsible for most of the photoinhibition in the species.

Sensitivity assessment. As the key structuring and characterizing species colonize a broad range of light environments from intertidal to deeper sub tidal and shaded understorey habitats the biotope is considered to have 'High' resistance and, by default, 'High' resilience and therefore is 'Not sensitive' to this pressure. A change in shading, greater than the pressure benchmark which severely reduced light penetration would negatively impact *Palmaria palmata* and other algae within the biotope. Very high light levels can also negatively impact algae through photoinhibition.

Barrier to species movement	High Q: Low A: NR C: NR	High Q: High A: High C: High	Not sensitive Q: Low A: Low C: Low

Barriers that reduce the degree of tidal excursion may alter larval supply to suitable habitats from source populations. Conversely the presence of barriers may enhance local population supply by preventing the loss of larvae from enclosed habitats. Barriers and changes in tidal excursion are not considered relevant to the characterizing red algal species dispersal is limited by the rapid rate of settlement and vegetative growth from bases rather than reliance on recruitment from outside of populations. Other species associated with the biotope are widely distributed and produce large numbers of larvae capable of long distance transport and survival, resistance to this pressure is assessed as 'High' and resilience as 'High' by default. This biotope is therefore considered to be

'Not sensitive'.

Death or injury by collision	Not relevant (NR) Q: NR A: NR C: NR	Not relevant (NR) Q: NR A: NR C: NR	Not relevant (NR) Q: NR A: NR C: NR

Not relevant' to seabed habitats. NB. Collision by grounding vessels is addressed under 'surface abrasion.

Visual disturbance	Not relevant (NR) Q: NR A: NR C: NR	Not relevant (NR) Q: NR A: NR C: NR	Not relevant (NR) Q: NR A: NR C: NR

Not relevant.

Biological Pressures

	Resistance	Resilience	Sensitivity
Genetic modification & translocation of indigenous species	Not relevant (NR) Q: NR A: NR C: NR	Not relevant (NR) Q: NR A: NR C: NR	Not relevant (NR) Q: NR A: NR C: NR

No information was found on current production of *Mastocarpus stellatus*, *Chondrus crispus* or other turf forming red seaweeds in the UK and it is understood that wild harvesting rather than cultivation is the method of production for these and littorinids. No evidence was found for the effects of gene flow between cultivated species and wild populations. Although cultivation of different genotypes may lead to gene flow between wild and cultivated populations the limited dispersal may reduce exposure. Some negative effects may arise from hybridisation between very geographically separated populations but there is no evidence to suggest that gene flow between different UK haplotypes would lead to negative effects. This pressure is therefore considered 'Not relevant' to this biotope group.

Introduction or spread of invasive non-indigenous species	Low Q: High A: High C: High	Very Low Q: Low A: NR C: NR	High Q: Low A: Low C: Low

Invasive non-indigenous species (INIS) that can alter habitats (ecological engineers), or out-compete native macroalgae for space and other resources such as light and nutrients, are the most likely species to negatively affect this biotope. Space pre-emption by holdfasts may prevent settlement of INIS until disturbance events create gaps for invasion. However, in the Mediterranean crustose corallines and algal turfs facilitate attachment of *Caulerpa racemosa* by providing a more complex substratum than bare rock (Bulleri & Benedetti-Cecchi, 2008).

Algal species which may have overlapping habitat requirements include the green seaweed *Codium fragile* subsp *tormentosoides* (now renamed as *Codium fragile fragile*) and the red seaweed *Heterosiphonia japonica*, neither of these have so far been recorded in nuisance densities (Sweet, 2011j). Wireweed, *Sargassum muticum and Grateloupia turuturu* gros best on sheltered shores and in rockpools (Sewell, 2011c, 2011g) and the wave exposed habitats where this biotope occurs may not be suitable for establishment. The red seaweeds *Heterosiphonia*

japonica and *Neosiphonia harveyi* may also occur in this biotope but, again, no impacts have been reported.

The tunicates *Didemnum vexillum* and *Asterocarpa humilis*, the hydroid *Schizoporella japonica* and the bryozoan *Watersipora subatra* (Bishop, 2012c, Bishop, 2015a and b; Wood, 2015) are currently only recorded from artificial hard substratum in the UK and it is not clear what their established range and impacts in the UK would be.

A significant potential INIS is the Pacific oyster *Magallana gigas*, as its distribution and environmental tolerances are considered to overlap with this biotope on moderately exposed shores, where this reef forming species can alter habitat structure. This species may also affect the grazers present in the biotope. In the Wadden Sea and North Sea, *Magallana gigas* overgrows mussel beds in the intertidal zone (Diederich, 2005, 2006; Kochmann *et al*., 2008).

The non-native crab *Hemigrapsus sanguineus* has recently been recorded in the UK (Sweet & Sewell, 2014) and has the potential to be a significant predator of intertidal invertebrates. Significant reductions in common shore crab abundance and mussel density have been reported where the Asian shore crab has achieved high densities in mainland Europe (Sweet & Sewell, 2014). In Rye, New York, declines of approximately 80% of *Littorina littorea* in the intertidal were reported to coincide with an expansion of the *Hemigrapsus sanguineus* population (Kraemer *et al*., 2007). This crab occurs on exposed shores and may therefore occur in this biotope when established.

Sensitivity assessment. Little evidence was found to assess the impact of INIS on this biotope and much of the evidence comes from intertidal habitats in other countries. The conversion of this biotope to a *Magallana gigas* reef on moderately exposed shores would present a significantly negative impact. Colonization of red algal turfs by other similar species may lead to some subtle effects on local ecology but at low abundances the biotope would still be recognisable from the description. Based on *Magallana gigas*, biotope resistance to this pressure is assessed as 'Low'. The biotope will only recover if these species are removed, either through active management or natural processes. To recognise that recovery may be prolonged, resilience is assessed as 'Very Low' and sensitivity is therefore assessed as 'High'. Where this biotope occurs on exposed or very exposed shores, the level of wave action may prevent colonization by *Magallana gigas*.

Introduction of microbial pathogens	High Q: High A: High C: High	High Q: High A: High C: High	Not sensitive Q: High A: High C: High

No evidence was found for pathogens of *Mastocarpus stellatus*, the key characterizing species. Craigie & Correa (1996) described 'green spot' disease in *Chondrus crispus*, caused by the interaction of several biotic agents including fungi, bacteria, algal endophytes and grazers, and resulting in tissue necrosis. Correa & McLachlan (1992) infected *Chondrus crispus* with the green algal endophytes *Acrochaete operculata* and *Acrochaete heteroclada*. Infections resulted in detrimental effects on host performance, including slower growth, reduced carrageenan yield, reduced generation capacity and tissue damage. Stanley (1992) described the fungus *Lautita danica* being parasitic on cystocarpic *Chondrus crispus* and Molina (1986) was the first to report *Petersenia pollagaster*, a fungal invasive pathogen of cultivated *Chondrus crispus*. At usual levels of infestation in wild populations these are not considered to lead to high levels of mortality.

Sensitivity assessment. Based on the lack of evidence for major pathogens and significant mortalities of *Mastocarpus stellatus* and other turf-forming macroalgae this biotope is considered to

have 'High' resistance and hence 'High' resilience and is classed as 'Not sensitive' at the pressure benchmark.

Removal of target species	Low Q: High A: High C: High	High Q: High A: High C: High	Low Q: High A: High C: High

Direct, physical impacts from harvesting are assessed through the abrasion and penetration of the seabed pressures. The sensitivity assessment for this pressure considers any biological/ecological effects resulting from the removal of target species on this biotope. Incidental removal of the key characterizing species and associated species would alter the character of the biotope. *Mastocarpus stellatus* and *Chondrus crispus* are both harvested commercially in Scotland and Ireland , the stipe is removed but the base is left intact to allow the algae to re-grow. *Palmaria palmata* and *Osmundea pinnatifida* are also collected by hand commercially and recreationally for for consumption. As the key characterizing and structuring species extensive removal of *Mastocarpus stellatus* and *Chondrus crispus* would alter the character of the biotope. The effect of harvesting *Chondrus crispus* has been best studied in Canada. Prior to 1980, the seaweed beds of Prince Edward Island were dominated by *Chondrus crispus* and the species was heavily exploited. Recently, there has been a marked increase in abundance of anotherred seaweed, *Furcellaria lumbricalis*, which is avoided by the commercial harvest, and an associated decline in abundance of *Chondrus crispus* (Sharp *et al.*, 1993). The authors suggested that harvesting has brought about the shift in community structure. Sharp *et al.* (1986) reported that the first drag rake harvest of the season, on a Nova Scotian *Chondrus crispus* bed, removed 11% of the fronds and 40% of the biomass. Efficiency declined as the harvesting season progressed. Chopin *et al.* (1988) noted that non-drag raked beds of *Chondrus crispus* in the Gulf of St Lawrence showed greater year round carposporangial reproductive capacity than a drag raked bed. In the short-term, therefore, harvesting of *Chondrus crispus* may remove biomass and impair reproductive capacity, while in the long-term, it has the potential to alter community structure and change the dominant species. Removal of other associated algae such as *Palmaria palmata* and *Osmundea pinnatifida* will reduce cover of turf forming red algae in this biotope.

The winkle *Littorina littorea* and the limpet *Patella vulgata* occur in low densities in this biotope and may be gathered by hand. Changes in grazer abundance can alter the character of the assemblage. Grazer removal (manual removal of all gastropods in pool and a 1m surrounding perimeter) caused strong and highly significant changes in assemblage structure in rockpools that contained red turf forming algae mainly due to an increase in the cover of green filamentous algae and a decrease in cover of live crustose coralline algae (25.40%) (Atalah & Crowe, 2010).

The removal of kelps or fucoids from this biotope would reduce shading and is not considered to negatively affect this biotope (for assessment of removal of the key characterizing species as by-catch, see the removal of non-target species pressure).

Sensitivity assessment. The species that are harvested in this biotope are all attached, sedentary or slow moving and relatively conspicuous. A single event of targeted harvesting could therefore efficiently remove individuals and resistance is assessed as 'Low'. This assessment is supported by evidence from Sharp *et al.*, (1993) on the proportion of biomass of *Mastocarpus stellatus* and *Chondrus crispus* removed commercially. Resilience of the turf forming red seaweeds is assessed as 'High' (based on evidence for recovery from harvesting that did not damage the algal bases although see caveats in the resilience section) and biotope sensitivity is assessed as 'Low'. This assessment refers to a single collection event, long-term harvesting over wide spatial scales will

lead to greater impacts, with lower resistance and longer recovery times. Intense harvesting of littorinids, coupled with removal of limpets would be likely to result in enhance growth of ephemeral algae based on Atalah & Crowe (2010).

Removal of non-target species	Low Q: Low A: NR C: NR	Medium Q: High A: High C: High	Medium Q: Low A: Low C: Low

Incidental removal of the turf of the key characterizing species and associated species would alter the character of the biotope. The biotope is characterized by a turf of *Mastocarpus stellatus* and other turf-forming red algae. The loss of the biological assemblage due to incidental removal as by-catch would therefore alter the character of the habitat and result in the loss of species richness. The ecological services such as primary production and the habitat provided by these species would also be lost. Changes in abundance of grazers and the creation of large areas of bare rock through the removal of basal crusts could lead to significant long-term changes in community composition and result in a higher sensitivity.

Sensitivity assessment. Removal of a large percentage of the characterizing species resulting in bare rock would alter the character of the biotope through removal of the turf, with consequent changes in species richness and ecosystem function. Resistance is therefore assessed as ‘Low’ and recovery as ‘High’ (where the basal crusts are not removed- see resilience section), so that sensitivity is assessed as 'Low'. If the basal crusts were removed sensitivity would be considered to be greater as recovery times would be longer.

Bibliography

Aguirre-von-Wobeser, E., Figueroa, F.L. & Cabello-Pasini, A., 2000. Effect of UV radiation on photoinhibition of marine macrophytes in culture systems. *Journal of Applied Phycology*, **12** (2), 159-168

Alströem-Rapaport, C., Leskinen, E. & Pamilo, P., 2010. Seasonal variation in the mode of reproduction of *Ulva intestinalis* in a brackish water environment. *Aquatic Botany*, **93** (4), 244-249.

Atalah, J. & Crowe, T.P., 2010. Combined effects of nutrient enrichment, sedimentation and grazer loss on rock pool assemblages. *Journal of Experimental Marine Biology and Ecology*, **388** (1), 51-57.

Barnes, H., Finlayson, D.M. & Piatigorsky, J., 1963. The effect of desiccation and anaerobic conditions on the behaviour, survival and general metabolism of three common cirripedes. *Journal of Animal Ecology*, **32**, 233-252.

Bhattacharya, D., 1985. The demography of fronds of *Chondrus crispus* Stackhouse. *Journal of Experimental Marine Biology and Ecology*, **91**, 217-231.

Bird, N.L., Chen, L.C.-M. & McLachlan, J., 1979. Effects of temperature, light and salinity of growth in culture of *Chondrus crispus*, *Furcellaria lumbricalis*, *Gracilaria tikvahiae* (Gigartinales, Rhodophyta), and *Fucus serratus* (Fucales, Phaeophyta). *Botanica Marina*, **22**, 521-527.

Bischof, K., Kräbs, G., Hanelt, D. & Wiencke, C., 2000. Photosynthetic characteristics and mycosporine-like amino acids under UV radiation: a competitive advantage of *Mastocarpus stellatus* over *Chondrus crispus* at the Helgoland shoreline? *Helgoland Marine Research*, **54** (1), 47-52.

Bokn, T.L., Moy, F.E. & Murray, S.N., 1993. Long-term effects of the water-accommodated fraction (WAF) of diesel oil on rocky shore populations maintained in experimental mesocosms. *Botanica Marina*, **36**, 313-319.

Boller, M.L. & Carrington, E., 2006. In situ measurements of hydrodynamic forces imposed on *Chondrus crispus* Stackhouse. *Journal of Experimental Marine Biology and Ecology*, **337** (2), 159-170.

Boller, M.L. & Carrington, E., 2007. Interspecific comparison of hydrodynamic performance and structural properties among intertidal macroalgae. *Journal of Experimental Biology*, **210** (11), 1874-1884.

Bowman, R.S. & Lewis, J.R., 1977. Annual fluctuations in the recruitment of *Patella vulgata* L. *Journal of the Marine Biological Association of the United Kingdom*, **57**, 793-815.

Bulleri, F. & Airoldi, L., 2005. Artificial marine structures facilitate the spread of a non-indigenous green alga, *Codium fragile* ssp. *tomentosoides*, in the north Adriatic Sea. *Journal of Applied Ecology*, **42** (6), 1063-1072.

Chopin, T. & Floc'h, J.-Y., 1992. Eco-physiological and biochemical study of two of the most contrasting forms of *Chondrus crispus* (Rhodophyta, Gigartinales). *Marine Ecology Progress Series*. **81** (2), 185-195.

Chopin, T., Pringle, J.D. & Semple, R.E., 1988. Reproductive capacity of dragraked and non-dragraked Irish moss (*Chondrus crispus* Stackhouse) beds in the southern Gulf of St Lawrence. *Canadian Journal of Fisheries and Aquatic Sciences*, **45**, 758-766.

Connor, D.W., Allen, J.H., Golding, N., Howell, K.L., Lieberknecht, L.M., Northen, K.O. & Reker, J.B., 2004. The Marine Habitat Classification for Britain and Ireland. Version 04.05. ISBN 1 861 07561 8. In JNCC (2015), *The Marine Habitat Classification for Britain and Ireland Version 15.03*. [2019-07-24]. Joint Nature Conservation Committee, Peterborough. Available from https://mhc.jncc.gov.uk/

Corradi, M.G., Gorbi, G. & Zanni, C., 2006. Hypoxia and sulphide influence gamete production in *Ulva* sp. *Aquatic Botany*, **84** (2), 144-150.

Correa, J.A. & McLachlan, J.L., 1992. Endophytic algae of *Chondrus crispus* (Rhodophyta). 4. Effects on the host following infections by *Acrochaete operculata* and *A. heteroclada* (Chlorophyta). *Marine Ecology Progress Series*, **81**, 73-87.

Craigie, J.S. & Correa, J.A., 1996. Etiology of infectious diseases in cultivated *Chondrus crispus* (Gigartinales, Rhodophyta). *Hydrobiologia*, **326-327**, 97-104.

Davenport, J. & Davenport, J.L., 2005. Effects of shore height, wave exposure and geographical distance on thermal niche width of intertidal fauna. *Marine Ecology Progress Series*, **292**, 41-50.

Davies, S.P., 1970. Physiological ecology of *Patella* IV. Environmental and limpet body temperatures. *Journal of the Marine Biological Association of the United Kingdom*, **50** (04), 1069-1077.

Dixon, P.S. & Irvine, L.M., 1977. *Seaweeds of the British Isles. Volume 1 Rhodophyta. Part 1 Introduction, Nemaliales, Gigartinales.* London: British Museum (Natural History) London.

Dudgeon, S. R., Davison. L R. & Vadas, R. L.,1989. Effect of freezing on photosynthesis of intertidal macroalgae relative tolerance of *Chondrus crispus* and *Mastocarpus stellatus* (Rhodophyta). *Marine Biology*, **101**, 107-114

Dudgeon, S.R. & Johnson, A.S., 1992. Thick vs. thin: thallus morphology and tissue mechanics influence differential drag and dislodgement of two co-dominant seaweeds . *Journal of Experimental Marine Biology and Ecology*, **165**, 23-43.

Dudgeon, S.R., Davison, I.R. & Vadas, R.L., 1990. Freezing tolerance in the intertidal red algae *Chondrus crispus* and *Mastocarpus stellatus*: relative importance of acclimation and adaptation. *Marine Biology*, **106**, 427-436.

Dudgeon, S.R., Kuebler, J.E., Vadas, R.L. & Davison, I.R., 1995. Physiological responses to environmental variation in intertidal red algae: does thallus morphology matter ? *Marine Ecology Progress Series*, **117**, 193-206.

Ekaratne, S.U.K. & Crisp, D.J., 1984. Seasonal growth studies of intertidal gastropods from shell micro-growth band

measurements, including a comparison with alternative methods. *Journal of the Marine Biological Association of the United Kingdom*, **64**, 183-210.

Fernandez, C. & Menendez, M.P., 1991. Ecology of *Chondrus crispus* on the northern coast of Spain. 2. Reproduction. *Botanica Marina*, **34**, 303-310.

Firth, L., Thompson, R., Bohn, K., Abbiati, M., Airoldi, L., Bouma, T., Bozzeda, F., Ceccherelli, V., Colangelo, M. & Evans, A., 2014. Between a rock and a hard place: Environmental and engineering considerations when designing coastal defence structures. *Coastal Engineering*, **87**, 122-135.

Fortes, M.D. & Lüning, K., 1980. Growth rates of North Sea macroalgae in relation to temperature, irradiance and photoperiod. *Helgolander Meeresuntersuchungen*, **34**, 15-29.

Foster, B.A., 1970. Responses and acclimation to salinity in the adults of some balanomorph barnacles. *Philosophical Transactions of the Royal Society of London, Series B*, **256**, 377-400.

Fretter, V. & Graham, A., 1994. *British prosobranch molluscs: their functional anatomy and ecology*, revised and updated edition. London: The Ray Society.

Green, D., Chapman, M. & Blockley, D., 2012. Ecological consequences of the type of rock used in the construction of artificial boulder-fields. *Ecological Engineering*, **46**, 1-10.

Grenon, J.F. & Walker, G., 1981. The tenacity of the limpet, *Patella vulgata* L.: an experimental approach. *Journal of Experimental Marine Biology and Ecology*, **54**, 277-308.

Guidone, M. & Grace, S., 2010. The ratio of gametophytes to tetrasporophytes of intertidal *Chondrus crispus* (Gigartinaceae) across a salinity gradient. *Rhodora*, **112** (949), 80-84.

Guiry, M.D. & Guiry, G.M. 2015. AlgaeBase [Online], National University of Ireland, Galway [cited 30/6/2015]. Available from: http://www.algaebase.org/

Gutierrez, L.M. & Fernandez, C., 1992. Water motion and morphology in *Chondrus crispus* (Rhodophyta). *Journal of Phycology*, **28**, 156-162.

Hammer, L., 1972. Anaerobiosis in marine algae and marine phanerograms. In *Proceedings of the Seventh International Seaweed Symposium, Sapporo, Japan, August 8-12, 1971* (ed. K. Nisizawa, S. Arasaki, Chihara, M., Hirose, H., Nakamura V., Tsuchiya, Y.), pp. 414-419. Tokyo: Tokyo University Press.

Harlin, M.M., & Lindbergh, J.M., 1977. Selection of substrata by seaweed: optimal surface relief. *Marine Biology*, **40**, 33-40.

Harvey, M.J. & McLachlan, J., 1973. *Chondrus crispus. Proceedings of the Transactions of the Nova Scotian Institute of Science*, **27** (Suppl.1), 1-155.

Hawkins, S.J. & Harkin, E., 1985. Preliminary canopy removal experiments in algal dominated communities low on the shore and in the shallow subtidal on the Isle of Man. *Botanica Marina*, **28**, 223-30.

Hiscock, K., 1983. Water movement. In *Sublittoral ecology. The ecology of shallow sublittoral benthos* (ed. R. Earll & D.G. Erwin), pp. 58-96. Oxford: Clarendon Press.

Hiscock, K., ed. 1998. *Marine Nature Conservation Review. Benthic marine ecosystems of Great Britain and the north-east Atlantic.* Peterborough, Joint Nature Conservation Committee.

Holt, T.J., Jones, D.R., Hawkins, S.J. & Hartnoll, R.G., 1995. The sensitivity of marine communities to man induced change - a scoping report. *Countryside Council for Wales, Bangor, Contract Science Report*, no. 65.

JNCC, 2015. The Marine Habitat Classification for Britain and Ireland Version 15.03. (20/05/2015). Available from https://mhc.jncc.gov.uk/

Johansson ,G., Eriksson, B.K., Pedersen, M. & Snoeijs, P., 1998. Long term changes of macroalgal vegetation in the Skagerrak area. *Hydrobiologia*, **385**, 121-138.

Juanes, J.A. & McLachlan, J.L., 1992. Productivity of *Chondrus crispus* Stackhouse (Rhodophyta, Gigartinales) in sublittoral Prince Edward Island. 2. Influence of temperature and nitrogen reserves. *Botanica Marina*, **35**, 399-405.

Kuebler, J.E. & Davison, I.R., 1993. High temperature tolerance of photosynthesis in the red alga *Chondrus crispus*. *Marine Biology*, **117**, 327-335.

Kuebler, J.E. & Dudgeon, S.R., 1996. Temperature dependent change in the complexity of form of *Chondrus crispus* fronds. *Journal of Experimental Marine Biology and Ecology*, **207**, 15-24.

Lindgren, A. & Åberg, P., 1996. Proportion of life cycle stages of *Chondrus crispus* and its population structure: a comparison between a marine and an estuarine environment. *Botanica Marina*, **39** (1-6), 263-268.

Lubchenco, J., 1980. Algal zonation in the New England rocky intertidal community: an experimental analysis. *Ecology*, **61**, 333-344.

Lüning, K., 1990. *Seaweeds: their environment, biogeography, and ecophysiology*: John Wiley & Sons.

MacFarlane, C.I., 1952. A survey of certain seaweeds of commercial importance in southwest Nova Scotia. *Canadian Journal of Botany*, **30**, 78-97.

Marshall, D.J. & McQuaid, C.D., 1989. The influence of respiratory responses on the tolerance to sand inundation of the limpets *Patella granularis* L.(Prosobranchia) and *Siphonaria capensis* Q. et G.(Pulmonata). *Journal of Experimental Marine Biology and Ecology*, **128** (3), 191-201.

Marshall, D.J. & McQuaid, C.D., 1993. Effects of hypoxia and hyposalinity on the heart beat of the intertidal limpets *Patella granvlaris* (Prosobranchia) and *Siphonaria capensis* (Pulmonata). *Comparative Biochemistry and Physiology Part A: Physiology*, **106** (1), 65-68

Mathieson, A. & Norall, T., 1975. Photosynthetic studies of *Chondrus crispus*. *Marine Biology*, **33** (3), 207-213.

Mathieson, A.C. & Burns, R.L., 1971. Ecological studies of economic red algae. 1. Photosynthesis and respiration of *Chondrus crispus* (Stackhouse) and *Gigartina stellata* (Stackhouse) Batters. *Journal of Experimental Marine Biology and Ecology*, **7**, 197-206.

Mathieson, A.C. & Burns, R.L., 1975. Ecological studies of economic red algae. 5. Growth and reproduction of natural and harvested populations of *Chondrus crispus* Stackhouse in New Hampshire. *Journal of Experimental Marine Biology and Ecology*, **17**, 137-156.

Minchinton, T.E., Schiebling, R.E. & Hunt, H.L., 1997. Recovery of an intertidal assemblage following a rare occurrence of scouring by sea ice in Nova Scotia, Canada. *Botanica Marina*, **40**, 139-148.

Molina, F.I., 1986. *Petersenia pollagaster* (Oomycetes): an invasive fungal pathogen of *Chondrus crispus* (Rhodophyceae). In *The Biology of Marine Fungi* (ed. S.T. Moss), 165-175.

Newell, R.C., 1979. *Biology of intertidal animals*. Faversham: Marine Ecological Surveys Ltd.

Norton, T.A., 1992. Dispersal by macroalgae. *British Phycological Journal*, **27**, 293-301.

Pratt, M. & Johnson, A. 2002. Strength, drag and dislodgement of two competing intertidal algae from two wave exposures and four seasons. *Journal of Experimental Marine Biology and Ecology*, **272**, 71-101.

Prince, J.S. & Kingsbury, J.M., 1973. The ecology of *Chondrus crispus* at Plymouth, Massachusetts. 3. Effect of elevated temperature on growth and survival. *Biology Bulletin*, **145**, 580-588.

Pringle, J., & Semple, R. 1980. The benthic algal biomass, commercial harvesting, and *Chondrus* growth and colonization off southwestern Nova Scotia. In *Proceedings of the workshop on the relationship between sea urchin grazing and commercial plant / animal harvesting*. Edited by J. Pringle, G. Sharp, and J. Caddy. Canadian Technical Report of Fisheries and Aquatic Sciences 954. pp. 144-169.

Pringle, J.D. & Mathieson, A.C., 1986. *Chondrus crispus* Stackhouse. *Case Studies of Seven Commercial Seaweed Resources*, **281**, 49-122, FAO Fisheries Technical Paper.

Pybus, C., 1977. The ecology of *Chondrus crispus* and *Gigartina stellata* (Rhodophyta) in Galway Bay. *Journal of the Marine Biological Association of the United Kingdom*, **57**, 609-628.

Reed, R.H. & Russell, G., 1979. Adaptation to salinity stress in populations of *Enteromorpha intestinalis* (L.) Link. *Estuarine and Coastal Marine Science*, **8**, 251-258.

Ribeiro, P.A., Xavier, R., Santos, A.M. & Hawkins, S.J., 2009. Reproductive cycles of four species of *Patella* (Mollusca: Gastropoda) on the northern and central Portuguese coast. *Journal of the Marine Biological Association of the United Kingdom*, **89** (06), 1215-1221.

Scrosati, R., Garbary, D.J. & McLachlan, J., 1994. Reproductive ecology of *Chondrus crispus* (Rhodophyta, Gigartinales) from Nova Scotia, Canada. *Botanica Marina*, **37**, 293-300.

Seed, R. & Suchanek, T.H., 1992. Population and community ecology of *Mytilus*. In *The mussel* Mytilus*: ecology, physiology, genetics and culture*, (ed. E.M. Gosling), pp. 87-169. Amsterdam: Elsevier Science Publ. [Developments in Aquaculture and Fisheries Science, no. 25.]

Sharp, G.J., Tetu, C., Semple, R. & Jones, D., 1993. Recent changes in the seaweed community of western Prince Edward Island: implications for the seaweed industry. *Hydrobiologia*, **260-261**, 291-296.

Sharp, G.J., Tremblay, D.M. & Roddick, D.L., 1986. Vulnerability of the southwestern Nova Scotia *Chondrus crispus* resource to handraking. *Botanica Marina*, **29**, 449-453.

Simpson, F.J. & Shacklock, P.F., 1979. The cultivation of *Chondrus crispus*. Effect of temperature on growth and carageenan production. *Botanica Marina*, **22**, 295-298.

Southward, A.J., Hawkins, S.J. & Burrows, M.T., 1995. Seventy years observations of changes in distribution and abundance of zooplankton and intertidal organisms in the western English Channel in relation to rising sea temperature. *Journal of Thermal Biology*, **20**, 127-155.

Stanley, S.J., 1992. Observations on the seasonal occurrence of marine endophytic and parasitic fungi. *Canadian Journal of Botany*, **70**, 2089-2096.

Storey, K.B., Lant, B., Anozie, O.O. & Storey, J.M., 2013. Metabolic mechanisms for anoxia tolerance and freezing survival in the intertidal gastropod, *Littorina littorea*. *Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology*, **165** (4), 448-459.

Tasende, M.G. & Fraga, M.I., 1999. The growth of *Chondrus crispus* Stackhouse (Rhodophyta, Gigartinaceae) in laboratory culture. *Ophelia*, **51**, 203-213.

Taylor, A. R. A., Chen, L. C. M., Smith, B. D., & Staples, L. S. 1981. Chondrus holdfasts in natural populations and in culture. In *Proceedings of the International Seaweed Symposium* **8**, 140-145.

Vadas, R.L., Keser, M. & Rusanowski, P.C., 1976. Influence of thermal loading on the ecology of intertidal algae. In *Thermal Ecology II*, (eds. G.W. Esch & R.W. McFarlane), ERDA Symposium Series (Conf-750425, NTIS), Augusta, GA, pp. 202-212.

Vermaat J.E. & Sand-Jensen, K., 1987. Survival, metabolism and growth of *Ulva lactuca* under winter conditions: a laboratory study

of bottlenecks in the life cycle. *Marine Biology*, **95** (1), 55-61.

Vidaver, W., 1972. Dissolved gases - plants. In *Marine Ecology. Volume 1. Environmental factors (3)*, (ed. O. Kinne), 1471-1490. Wiley-Interscience, London.